

## Life History of a Hydroid/Nudibranch Association: A Discrete-Event Simulation

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**Abstract.** The general paradigm for early community succession is that early colonists do not replace themselves. Hydroids are typical early colonists that play an important role in the recruitment of later species. Aeolid nudibranchs are important predators on hydroids, and may thus have an indirect impact on succession. In an attempt to understand the mechanics of community change, we modeled nudibranch-hydroid community dynamics using a discrete-event simulation. Data for the model was obtained from life history studies of the aeolid nudibranch *Tenellia adspersa* (Nordmann, 1845) and its hydroid prey *Cordylophora lacustris* (Allman, 1853).

Seven simulations were performed, varying adult immigration, emigration, and larval settlement. The results of these simulations have important implications for early community succession and the role of nudibranchs in the persistence of hydroid colonies. In all simulations, the hydroid colony was completely removed by *T. adspersa*. *Cordylophora lacustris* persisted for the longest time in simulations with no adult migration or larval settlement. In addition, nudibranchs persisted for up to 46 days after their food supply was exhausted.

These predictions suggest that *Tenellia adspersa* can play an important indirect role in succession by removing hydroids and preventing their re-establishment.

### INTRODUCTION

The general paradigm for early community succession is that early colonists do not replace themselves (Connell, 1975). Connell (1978) suggested that succession could vary depending on factors such as disturbance, competitive interactions, and temporal availability of propagules. Connell & Slatyer (1977) proposed that established species could inhibit, facilitate, or remain neutral in the recruitment of later successional stage species.

Hydroids are typical early colonists in fouling communities; they tend to be succeeded by other species such as barnacles, tunicates, and mussels (Harris & Irons, 1982). Hydroids often have ephemeral life-history and distribution patterns, but can be important in affecting the recruitment of later successional species (Standing, 1976; Chester, 1996a).

The majority of aeolid nudibranchs are partial predators, consuming portions of hydroid colonies (Todd, 1981; Todd, 1983). Aeolid nudibranchs play a significant role in structuring hydroid communities (Harris, 1987). Aeolid predation can create physical gaps in prey colonies, alter the population structure, or cause changes in the prey's growth form (Gaulin et al., 1986). The impact of nudibranchs on hydroid colonies varies in relation to the number of predators in the colony. In low numbers,

the impact may be limited because the hydroid colony can grow faster than the nudibranch predation rate. However, at higher abundance, the impact is more substantial and will ultimately lead to the removal of the hydroid colony.

A number of aeolid species have life histories with short generation times and high reproductive output, which enable them to take advantage of temporally unpredictable, but often abundant, food resources. Most of these species have an obligate planktotrophic larval stage capable of remaining in the plankton for weeks to months. At least one of them, *Tenellia adspersa* (Nordmann, 1845), has lecithotrophic larvae that are capable of metamorphosing within the egg capsule (Chester, 1996b). This has important implications for nudibranch population growth within a hydroid colony and for the persistence of that colony. For populations of aeolids having pelagic larval stages, population growth in a hydroid colony will be determined by settlement and metamorphosis of larvae from the plankton. For aeolids having capsular development (or non-pelagic lecithotrophic development), population growth following initial recruitment will be determined by growth and reproductive rates of resident individuals within a hydroid colony. In the latter case, the aeolid's populations will increase at an exponential rate, inundating the hydroid colony and consuming it in a relatively short time.

*Tenellia adspersa* is a small (5–7 mm) aeolid nudibranch commonly found in New England estuarine en-

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vironments (Clark, 1975). *Tenellia adspersa* is a generalist that feeds on a variety of gymnoblastic and calyp-toblastic hydroids. Most of these hydroids are seasonally abundant in the Great Bay Estuary, New Hampshire (70°55'N, 43°5'W), existing as colonies on piers, floating docks, eelgrass blades, and other natural and artificial structures. In the estuary, the distribution and abundance of these hydroids can change within as little as one week's time (Chester, 1996a). *Tenellia adspersa* has a plastic developmental mode where both pelagic lecitho-trophic larvae and benthic juveniles are produced in the same spawn mass and by the same individual (Eyster, 1979; Chester, 1996b).

This study explores the implications of nudibranch life history on the persistence of a hydroid colony. The goal of this study was to design a computer simulation that would model hydroid-nudibranch dynamics. The study involves both laboratory studies and computer models of the nudibranch-hydroid system.

## MATERIALS AND METHODS

The hydroid, *Cordylophora lacustris* (Allman, 1853), was collected in September 1991 from a floating dock on the Oyster River, Durham, New Hampshire (70°55'N, 43°08'W). Colonies were cultured on glass slides that were suspended in aquaria at 25°C and at a salinity of 15–25‰. A small portion of a colony ( $\approx 3$  polyps) was placed under a monofilament line that was tightly wrapped around the slide. Colonies were fed nauplii of *Artemia salina* every other day.

The nudibranch *Tenellia adspersa* was collected in October 1991 from within *C. lacustris* colonies on a floating dock on the Squamscott River, Rockingham, New Hampshire (70°56'N, 43°02'W). Stock cultures were established in fingerbowls at 25°C and 25‰ and provided with an *ad libitum* amount of *C. lacustris*.

For the computer simulation comparing nudibranch and hydroid dynamics, the following observations were gathered: (1) measurement of hydroid colony growth, (2) determination of nudibranch life history, and (3) measurement of predation rates on hydroid colonies. These data were used to construct a discrete-event simulation model (Banks et al., 1996) of nudibranch population dynamics within a single hydroid colony. This type of model deals with individuals rather than aggregate behavior, thus it provides a finer-grained simulation than typical analytical models. It treats time as discrete units, with events determining its passage; thus, it simplifies the model enough to be tractable. Discrete-event simulation is often performed when the system being simulated is very complex, when some of the information needed for an analytical model is missing, or when it is important to track the effects of individual differences in simulated entities.

## Hydroid Colony Growth

Small pieces of *C. lacustris* containing approximately three polyps were attached to glass slides and suspended in aquaria at 20 and 25‰, with 10 replicates per salinity. These colonies were fed *A. salina* nauplii every other day. The number of polyps was counted every few days, and each colony was mapped at 60 $\times$  using a Wild dissecting microscope equipped with a drawing tube. Stolon length was measured with a map measurer, and the distance converted to the nearest 0.1 mm. In *C. lacustris*, stolons and uprights grow at a fairly constant rate (Fulton, 1963). Therefore, the inside diameter of stolon was measured to the nearest 1  $\mu$ m from histological cross-sections with a compound microscope equipped with an ocular micrometer (diameter =  $294 \pm 2$   $\mu$ m,  $n = 10$ ), and this value was used to calculate volume of stolon.

## Nudibranch Life History

Five newly laid spawn masses from *Tenellia adspersa* were haphazardly collected from the stock culture and raised with an *ad libitum* amount of *C. lacustris* in the same conditions as the stock culture. Water was changed daily and the number of nudibranchs recorded. Daily observations were made on nudibranch body length, number of spawn laid and number of eggs per spawn with a binocular dissecting microscope equipped with an ocular micrometer.

## Nudibranch Feeding Rates

In order to measure feeding rates, nudibranchs of various sizes were placed in colonies of *C. lacustris* and followed over time. The number of polyps was counted daily and the amount of living stolon measured as with the hydroid colony growth. The feeding rate was calculated as the change in living stolon, and represents the amount of growth less the amount eaten by the nudibranch.

## Discrete-Event Simulation Model

A discrete-event simulation model (e.g., Banks et al., 1996) was constructed to model nudibranch population dynamics. In the current case, the individuals modeled were nudibranchs. The information modeled per nudibranch included: time of birth, time of metamorphosis, number of spawn (egg masses), current reproductive rate (spawn/day, eggs/spawn), starvation status (including duration of starvation), and reproductive shut-off due to starvation. These parameters were changed during the simulations depending on the amount of food available to each nudibranch.

As our primary goal was to model the effect of individual nudibranchs on a hydroid colony, the hydroid colony was treated as a bulk food source. The amount of the hydroid was updated at the end of each simulated day



Table 1

Parameters used in the discrete-event simulation experiments. Values were obtained from the laboratory growth and feeding experiments.

Parameter	Nudibranchs fed		Nudibranchs starved	
	Mean	Std. Err.	Mean	Std. Err.
Adult lifespan (days)	24.5	1.0		
Time to metamorphosis (days)	7.1	0.2		
Time to first spawn (days)	17.6	0.3		
Number of spawn/day	5.4	0.9	0.3	0.3
Eggs per spawn	32.1	0.6	27.7	1.7
Hatching time (days)	6.3	0.2	4.8	0.3
Day of first feeding	5.0			
Percent of spawn that hatch	100.0			
Percent pelagic lecithotrophic larvae	76.8			
Hydroid growth rate (%/day)	21.2	1.4		
Feeding rate (mm hydroid/day * nudibranch) by nudibranch size				
0–1 mm	0.3	0.1		
1–2 mm	4.7	1.3		
2–3 mm	4.9	1.2		
3–4 mm	7.4	2.2		
> 4 mm	18.0	1.9		

based on the hydroid's growth that day and the total amount eaten by all nudibranchs.

The parameters used in the simulations were based on the laboratory experiments and are shown in Table 1. All parameters were held constant across simulation experiments except the independent variables: immigration rate  $4(I)$ , emigration rate ( $E$ ), and larval settlement rate ( $S$ ). Each simulation started with two adult nudibranchs and was allowed to run either for 80 days or until there were no events in the simulator's event queue other than "housekeeping" events (such as data collection). This corresponded to the situation of there being no nudibranchs of any life stage other than pelagic veligers in the system. The dependent variables of interest were  $N_{end}$ , the number of nudibranchs remaining alive at the end of the experiment, and  $t_d$ , the time between food source extinction and nudibranch population extinction (in the cases where  $N_{end} = 0$ ). Seven simulation experiments were performed as follows:

- $S_0I_0E_0$ : No immigration or emigration of adults, no larval settlement (in all experiments, hatched veligers were assumed to enter the plankton). This is similar to the laboratory experiments.
- $S_cI_0E_0$ : No immigration or emigration of adults, but larval settlement at a rate of one to three veligers per day ( $2.0 \pm 0.1$ ), which is consistent with what was observed in the Great Bay Estuary during the peak summer months (Chester, personal observation).
- $S_cI_0E_c$ : No immigration or emigration when food was present; emigration (10% per day) when

no food is available; and larval settlement at the rate above with or without food.

- $S_{fI_0E_c}$ : Same as  $S_cI_0E_c$ , except that larval settlement occurred only when food was present. This might correspond, for example, to an isolated population of nudibranchs where no other populations are close enough to allow immigration, but where veligers are present in the water column.
- $S_cI_cE_c$ : Immigration of  $2.0 \pm 0.1$  adults per day, random ages; a constant, low emigration rate (1% per day); and larval settlement. All occurred regardless of food source status.
- $S_{cI_fE_c}$ : Immigration at the above rate only when food is present; low emigration rate (1% per day) when food is present and a higher rate (10% per day) when food is exhausted; and larval settlement at the rate above regardless of food status.
- $S_{fI_fE_c}$ : Same as simulation  $S_{cI_fE_c}$ , except that larval settlement occurs only when food is present. This is conjectured to be similar to the case in the field.

Simulations were run both using the means of all parameters (the "means-only" case) and using the standard errors to determine normal distributions of the parameters (the "normal-distribution" case). It should be noted that even in the means-only runs, there is still some variation due to the means of integer parameters (e.g., eggs/spawn) being real numbers. In these cases, a probabilistic rounding scheme was used. Fifty simulations were run for each

case of each experiment, and the results averaged. Initial food supply in the means-only case was sufficient for 15 nudibranchs for one day, whereas in the normal-distribution case it was roughly half that, sufficient for seven nudibranchs for one day. This was because with the larger amount of food, in the normal-distribution case occasionally the population would become too large to simulate practically on the available computers.

### Statistical Analysis

Statistical analyses of the laboratory studies were performed using SYSTAT (vers. 5.03, Systat Inc., Evanston, Illinois). The relationship between nudibranch size and predation rates was investigated with an analysis of variance model (ANOVA) (Sokal & Rohlf, 1981; Zar, 1996). Tukey HSD was used to compare nudibranch sizes with different feeding rates. The discrete-event simulation results were analyzed using CLASP (Common Lisp Analytical Statistics Package) (Anderson et al., 1994). Means and standard errors are used throughout.

## RESULTS

*Tenellia adspersa* is a small nudibranch, reaching a maximum size of 6–8 mm. The body bears five to seven clusters of cerata, usually with two to three cerata per cluster. Cnidosacs are present at the tips of each cerata. The tip of the penis is armed and bears a cuticular stylet.

### Hydroid Colony Growth

The most rapid growth in *Cordylophora lacustris* occurred at 20‰ salinity (Figure 1A, B). Higher increase in the number of polyps occurred at 20‰, with slower growth at 25‰ (Figure 1A). This corresponds to an  $18.1 \pm 0.5$  percent increase at 20‰ and a  $4.5 \pm 0.4$  percent increase at 25‰. Stolon growth closely followed growth of polyps, with the more rapid growth occurring at 20‰ (Figure 1B). At these salinities, stolons grew 2–3 mm<sup>3</sup>/day. Slower growth occurred at 25‰ (stolon growth:  $0.5 \pm 0.3$  mm<sup>3</sup>/day). The percent change in volume of stolon was  $21.2 \pm 1.4$  at 20‰ and  $7.2 \pm 0.4$  at 25‰.

### Nudibranch Life History

The results of the life history study are presented in Figure 2. The generation time from egg to egg was approximately  $17.6 \pm 0.3$  days ( $n = 20$ ) and the life cycle from egg to death was  $24.5 \pm 1.0$  days ( $n = 10$ ). Hatching occurred in  $6.3 \pm 0.2$  days ( $n = 56$ ). Larvae metamorphosed in  $7.1 \pm 0.2$  days ( $n = 45$ ) at a juvenile size of  $0.3 \pm 0.1$  mm ( $n = 20$ ). *Tenellia adspersa* grew exponentially in size until sexual maturity, as observed by the presence of the first spawn mass. Size at maturity was  $4.5 \pm 0.2$  mm ( $n = 20$ ). The growth rate decreased after sexual maturity until a maximum length of  $6.1 \pm 0.3$  ( $n = 10$ ) was achieved. Nudibranchs decreased in size near

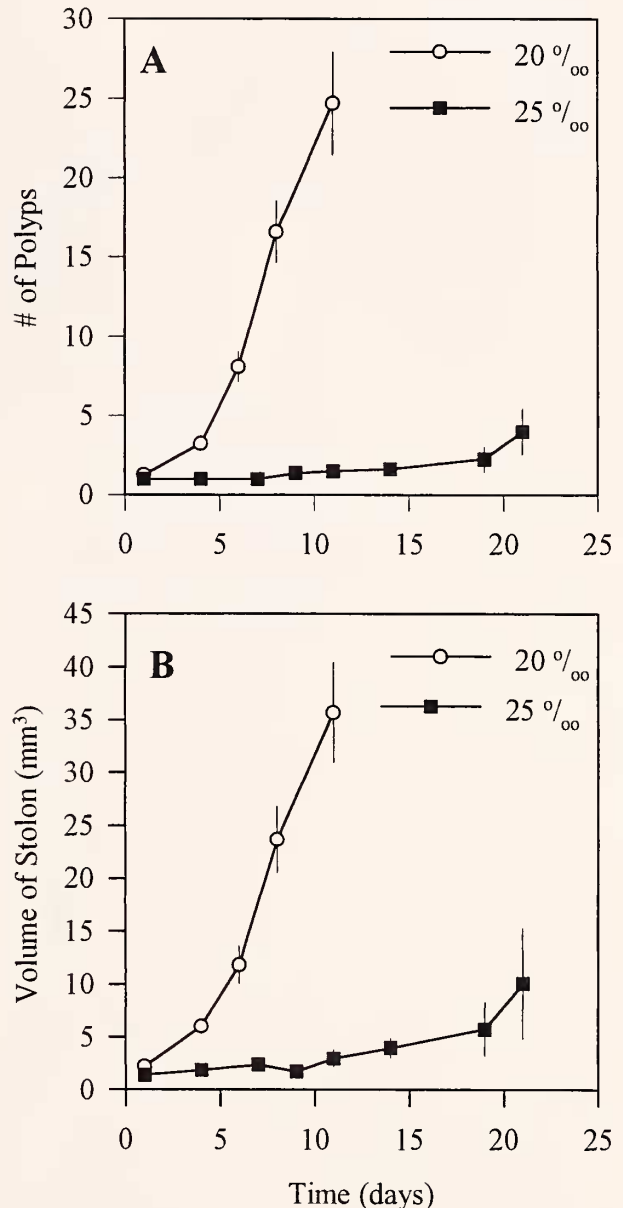


Figure 1

Growth of *Cordylophora lacustris* at two salinities, measured as number of polyps (A), and volume of stolon (B).

the end of their life, reaching a length of  $5.4 \pm 0.3$  mm ( $n = 10$ ). This decrease became apparent up to 7 days before death.

Mature nudibranchs produced  $5.4 \pm 0.9$  spawn masses per day ( $n = 10$ ) with  $32.1 \pm 0.6$  eggs per spawn ( $n = 10$ ). Their lifetime fecundity was  $39.4 \pm 7.6$  spawn per individual ( $n = 10$ ) for a total of  $1269.3 \pm 102.9$  eggs per individual ( $n = 10$ ).

### Nudibranch Feeding Rate

The results of the predation experiments are presented in Table 1 and Figure 3. *Tenellia adpersa* feeds by piercing the perisarc of the stolon with its radula and sucking out tissue. Larger nudibranchs (> 6 mm) were observed to feed on the polyps themselves by rasping bites out of the polyp. Newly metamorphosed juveniles were invariably found near new hydroid growth. No observable loss of hydroid tissue was observed for the first 4–5 days following metamorphosis. Nudibranchs ate significantly more polyps and more coenosarc as they grew (ANOVA: polyp predation,  $F_{4,21} = 168.0$ ,  $P < 0.0001$ ; stolon predation,  $F_{4,24} = 22.9$ ,  $P < 0.0001$ ) (Figure 3). Mature nudibranchs (> 4 mm) consumed  $18.0 \pm 1.9 \text{ mm}^3$  of stolon tissue per day and  $6.6 \pm 0.2$  polyps per day.

### Discrete-Event Simulation Experiments

Figures 4 and 5 illustrate the output of the simulator for each experiment. The results, including the maximum nudibranch population sizes, are summarized in Table 2. Each experiment is discussed briefly below:

Experiment  $S_oI_oE_o$ . In the means-only case (Figure 4A), the nudibranch population went extinct long after the food supply was exhausted ( $t_d = 24.4 \pm 0.3$  days). This difference between the two extinction times was significant (two-tailed t-test,  $P < 0.0001$ ). The population remained stable after the last spawn had hatched until about 45 days, then dropped rapidly to zero. In the normal distribution case (Figure 4B), there were remnants of the population that remained alive in some of the runs, giving  $N_{\text{end}} = 0.5 \pm 0.5$ . There appears to be two generations of nudibranchs as opposed to one in the means-only case as observed by two peaks in spawn masses. In this case as well, the nudibranch population outlived the hydroid by a large, significant time ( $t_d = 45.9 \pm 0.8$ ,  $P < 0.0001$ ). The fact that  $t_d$  in this case is greater than the mean lifespan of the nudibranchs is due in part to the presence of spawn that hatched following food exhaustion.

Experiment  $S_iI_oE_o$ . The graph of the means-only case was very similar to that of experiment  $S_oI_oE_o$ , except that there was still a small, nearly constant nudibranch population ( $N_{\text{end}} = 34$ ) present at the end of the experiment due to a constant influx of larvae from the plankton. This is also true of the normal-distribution case ( $N_{\text{end}} = 44.0 \pm 0.6$ ).

Experiment  $S_oI_oE_s$ . In the means-only case (Figure 4C), the population decreased smoothly until about day 43, at which point there is a fast decline. This is most likely due to nudibranchs beginning to die off and emigrate. There is a small, nearly constant population of nudibranchs ( $N_{\text{end}} = 14.9 \pm 0.2$ ) left at the end of the experiment. The normal-distribution case is similar, with  $N_{\text{end}} = 20.5 \pm 0.4$  (Figure 4D).

Experiment  $S_iI_oE_s$ . Both the means-only (Figure 4E) and the normal-distribution cases (Figure 4F) were very

similar to their counterparts in  $S_oI_oE_s$ , except that the nudibranchs became extinct in both cases long after the food was exhausted ( $t_d = 24.9 \pm 0.1$  and  $30.7 \pm 0.6$ , respectively,  $P < 0.0001$ ).

Experiment  $S_iI_cE_c$ . Both the means-only (Figure 5A) and the normal distribution case (Figure 5B) show virtually no decrease in nudibranchs after the final build-up of the population once the food is exhausted. Immigration, emigration, and larval settling seem to balance each other when coupled with the constant small number of spawn produced by the nudibranchs. Whether this case has biological significance is questionable, as it is unclear if spawn would be produced by the emigrating nudibranchs in the absence of food.

Experiment  $S_oI_cE_c$ . Both the means-only (Figure 5C) and the normal distribution (Figure 5D) show much the same pattern as  $S_oI_oE_c$ : a smooth decline in population from its peak, followed by a more precipitous decline (in means-only case) to a low, constant value ( $N_{\text{end}} = 14.8 \pm 0.1$  means-only,  $21.2 \pm 0.5$  normal-distribution).

Experiment  $S_iI_cE_c$ . (Figure 5E, F). This experiment shows much the same pattern as the preceding one except that the population goes to zero in both cases long after the food is exhausted ( $t_d = 24.1 \pm 0.1$  means-only,  $32.7 \pm 0.4$  normal-distribution).

### DISCUSSION

The computer model predicts several things about the behavior of the nudibranch-hydroid system. One prediction is that *Cordylophora lacustris* will not survive predation by *Tenellia adpersa*, based on the hydroid/nudibranch growth rates and nudibranch predation rates used in the models. *Cordylophora lacustris* persists for the longest time under conditions of no adult migration (immigration or emigration) or larval settlement (experiment  $S_oI_oE_o$ ) or with only larval settlement (experiment  $S_iI_oE_o$ ). Once adult immigration is taken into account, either through constant immigration (experiment  $S_iI_cE_c$ ) or through immigration only when hydroid remains (experiments  $S_oI_cE_c$  and  $S_iI_cE_c$ ), *C. lacustris* persists a fraction of the time.

This appears consistent with field and laboratory observations. For example, laboratory populations of *C. lacustris* colonies initially containing  $86.8 \pm 9.7$  polyps persisted for  $9.0 \pm 1.1$  days with four juvenile *T. adpersa* ( $n = 4$ ). In addition, Turpaeva (1963) demonstrated that a single individual of *Tenellia adpersa* could destroy a colony of the hydroid, *Perigonimus megas* consisting of up to 100 polyps in as short as 24 hours.

Another prediction of the simulations is that in all cases nudibranchs will persist for a long time after their food supply is exhausted, even under conditions that most closely mimic field conditions. This has implications for successional change within fouling communities. Not only will the nudibranchs destroy the hydroid colony, but also their presence prevents recolonization by hydroids.



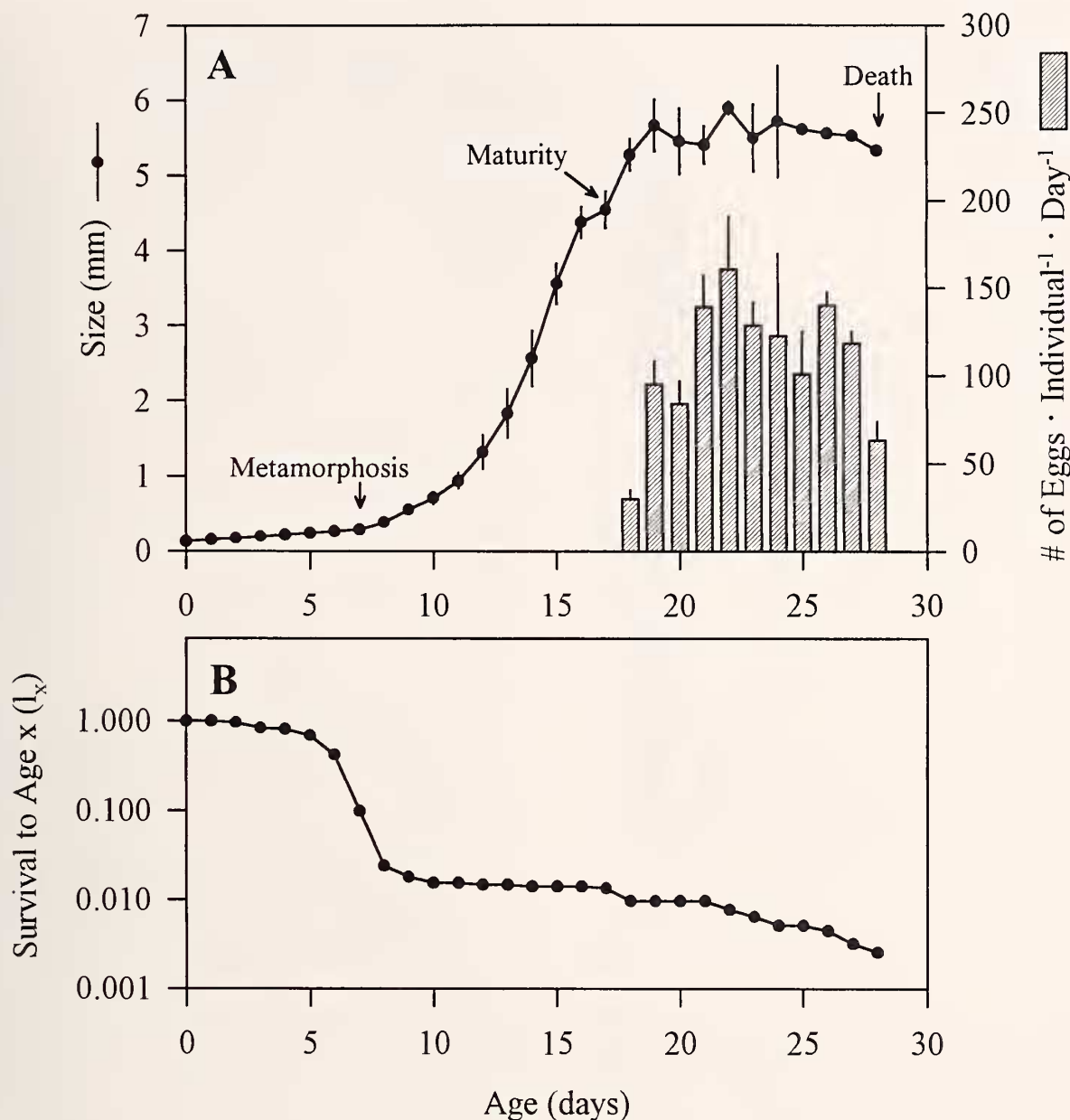


Figure 2

Nudibranch size and fecundity (A) and survivorship data (B) for *Tenellia adspersa* raised on *Cordylophora lacustris* at 30‰ salinity and 25°C.

This may help to explain why hydroids are often ephemeral and tend to be succeeded by other species. In addition, this suggests that nudibranchs may indirectly affect the successional process by removing hydroids and preventing their re-establishment. *Tenellia adspersa* may also have an effect on this process because of its feeding mechanisms. *Tenellia adspersa* predominantly feeds by piercing the perisarc and sucking out the tissue contents.

The perisarc is not eaten and typically remains behind. Although the three-dimensional structure, and hence effects on current flow over the colony, could remain much the same, a healthy hydroid colony, with its polyps intact, will very likely impede or facilitate settling of larvae quite differently than will its skeleton (Standing, 1976).

A third prediction is that in the presence of constant larval settlement (experiments  $S_cI_0E_0$ ,  $S_cI_0E_c$ ,  $S_cI_cE_c$ , and

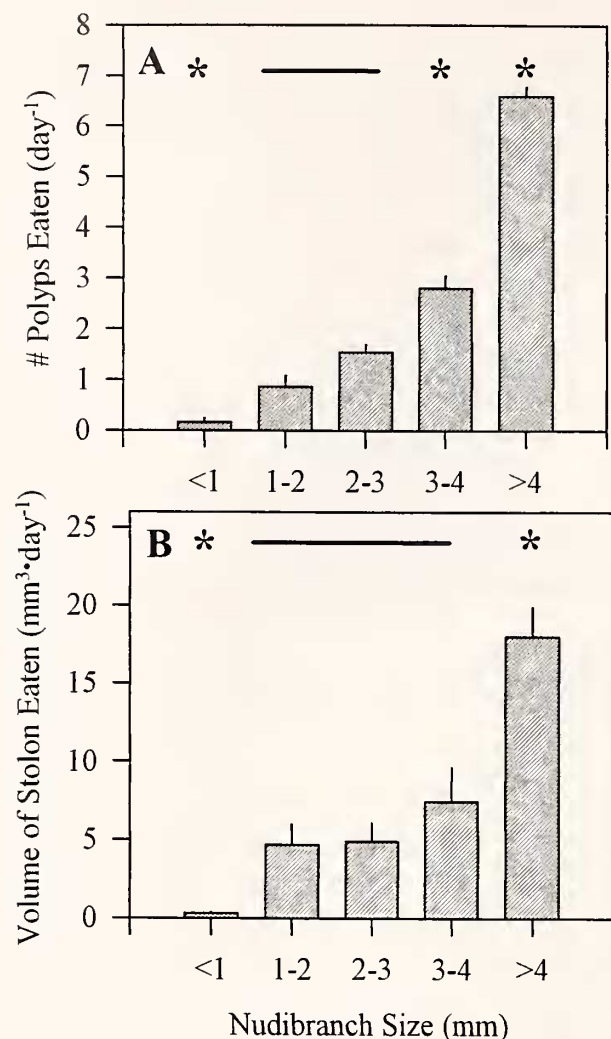


Figure 3

Predation rates for *Tenellia adpersa* feeding on *Cordylophora lacustris* in terms of number of polyps eaten per day (A) and volume of stolon eaten per day (B). The results of a Tukey HSD are presented as an asterisk if significantly different, and lines if not significantly different at  $\alpha = 0.05$  level.

$S_{cI}E_c$ ), nudibranchs will be present in an area no matter what the status of the hydroid colony. The nudibranch growth studies revealed that newly metamorphosed slugs persist for several days before visibly feeding on the hydroid. If there is no other food supply available, it is unlikely these nudibranchs will survive to adulthood. However, the presence of a steady supply of juvenile nudibranchs will prevent recolonization by hydroids.

The hydroid, *Cordylophora lacustris*, lives in fresh or brackish water conditions and can tolerate greater fluctuations in its habitat than its marine relatives (Fulton, 1962). In the Great Bay Estuary, *C. lacustris* is only

found in lower salinity riverine systems (15–20‰ or less) and does not occur within the Great Bay (Chester, personal observation). Although not performed under a range of salinities, the hydroid growth study tends to support these observations. Higher growth rate in terms of both number of polyps and volume of stolon occurred at 20‰ salinity with slower growth occurring at 25‰. Under controlled conditions, using defined media, Fulton (1960) grew colonies of *Cordylophora lacustris* and found that polyps increased exponentially with a doubling time of 3 days. Stolons grew linearly with a growth rate of 0.1 mm/hr (Fulton, 1963). This translates to a change in volume of 1.5 mm<sup>3</sup>/day (using a stolon diameter of 0.2 mm [Fulton, 1961]). The present study yielded values higher than Fulton's (1961) for the hydroid in 20‰.

The growth dynamics of *Tenellia adpersa* presented in this study are similar to those found by Harris et al. (1980) and Rasmussen (1944). However, the generation time and life cycle were shorter than previously observed. This may be a result of varying laboratory conditions. *Tenellia adpersa* grew exponentially until about the time of the first spawn mass. Growth rates decreased until about the 24th day when growth rates were negative. As with previous studies, fecundity varied greatly among individuals.

*Tenellia adpersa* produces both pelagic lecithotrophic larvae and capsular metamorphic juveniles, so some of the offspring will remain within the hydroid colony. This was accounted for in the simulations. Coupled with the short generation time observed (2–3 weeks), nudibranchs will build up within a colony very quickly as observed in the simulations. This will affect predation rates and ultimately the persistence of the hydroid colony.

The taxonomy of *Tenellia* is confusing. There appears to be at least two species of *Tenellia* along the Atlantic coast; *Tenellia fuscata* (Gould, 1870) and *Tenellia adpersa* (Nordmann, 1845). A third name, *Tenellia pallida* (Alder & Hancock, 1854) is a synonym of *T. adpersa* (Roginskaya, 1970). *Tenellia fuscata* possesses a muscular hermaphroditic duct consisting of a set of muscular sphincters located in the anterior portion of the oviduct (Chambers, 1934), lacks an armed penis, and lacks cnidosacs (Marcus & Marcus, 1960). The penis of *Tenellia adpersa* possesses a cuticular stylet (Chambers, 1934; Marcus & Marcus, 1960) as well as the presence of small cnidosacs at the tips of the cerata (Roginskaya, 1970; Brown, 1980). All of the available evidence, including radula morphology indicates that the name *Tenellia adpersa* is justified (Gosliner, personal communication).

The pattern described in these simulations for this specific nudibranch-hydroid association is consistent with the general model that early colonists do not replace themselves (Connell, 1975). The mechanism for this pattern is the accumulation of predators that consume the colonists and persist long enough to both inhibit re-establishment of the colonists and to facilitate the development of later

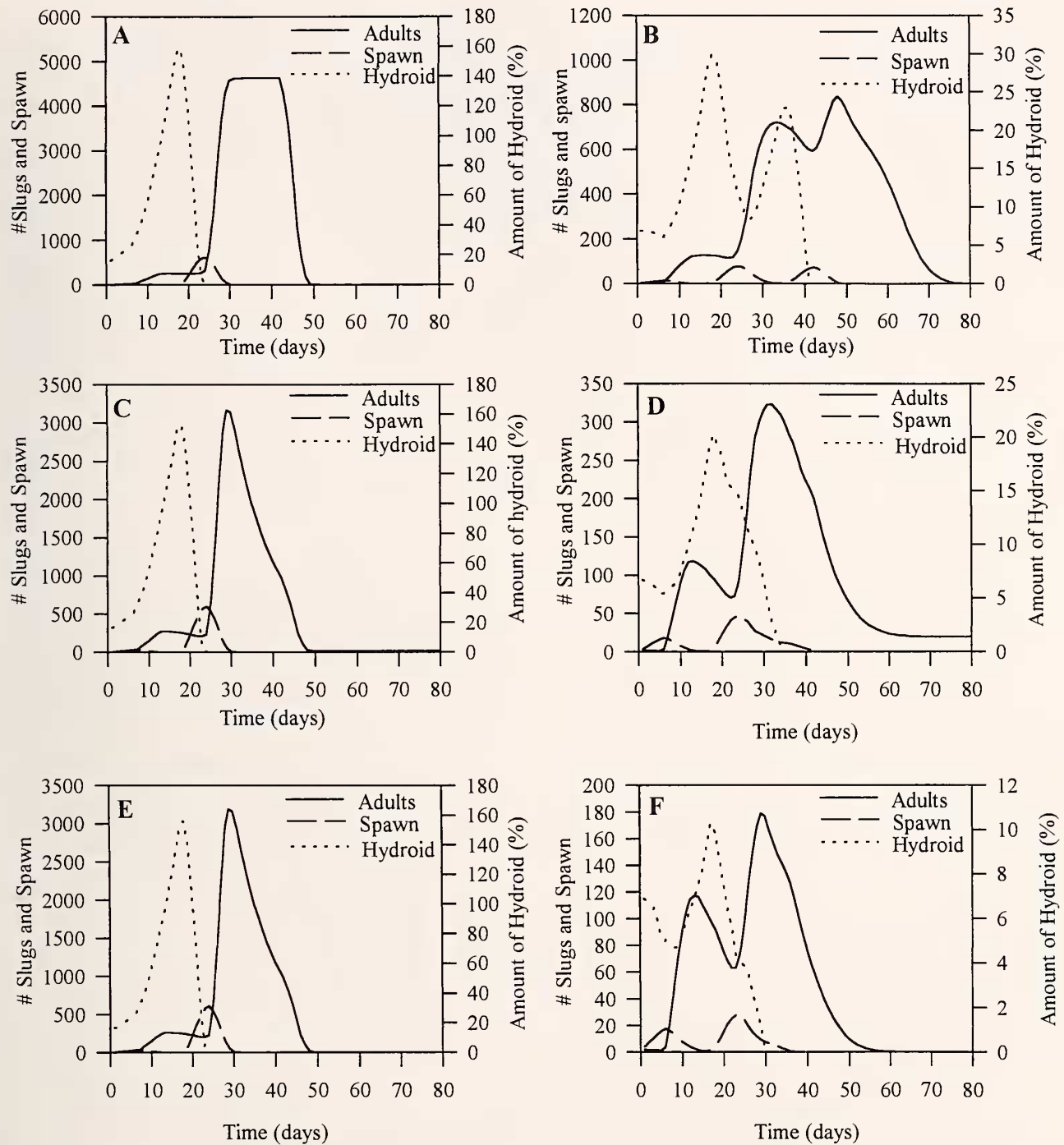


Figure 4

Results of discrete-event simulations: (A)  $S_0I_0E_0$  means-only, no larval settlement, no immigration, and no emigration, (B)  $S_0I_0E_0$  normal distribution, no larval settlement, no immigration, and no emigration, (C)  $S_0I_0E_0$  means-only, continuous settlement, no immigration, and no emigration, (D)  $S_0I_0E_0$  normal distribution, continuous settlement, no immigration, and no emigration, (E)  $S_0I_0E_0$  means-only, continuous settlement, no immigration, and emigration during starvation, (F)  $S_0I_0E_0$  normal distribution, continuous settlement, no immigration, and emigration during starvation.



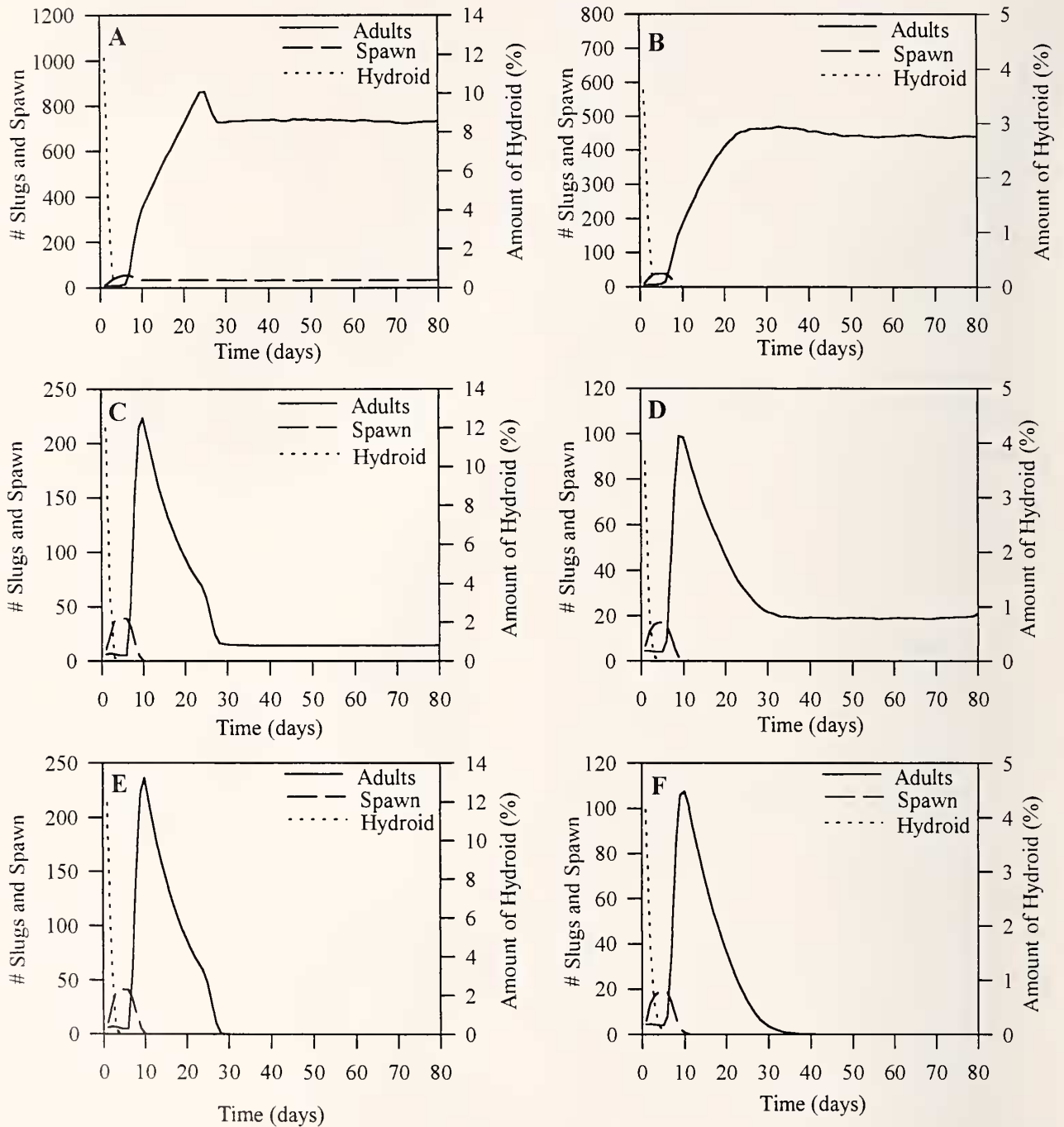


Figure 5

Results of discrete-event simulation: (A)  $S_0I_0E_0$  means-only, settling only when food is present, no immigration, and emigration when starving, (B)  $S_0I_0E_0$  normal distribution, settling only when food is present, no immigration, and emigration when starving, (C)  $S_0I_0E_0$  means-only, continuous settlement, immigration, and emigration, (D)  $S_0I_0E_0$  normal distribution, continuous settlement, immigration, and emigration, (E)  $S_0I_0E_0$  means-only, continuous settlement, immigration when food is present, emigration increased during starvation (F)  $S_0I_0E_0$  normal distribution, continuous settlement, immigration when food is present, emigration increased during starvation.

Table 2

Results of the simulation experiments. S = larval settlement, I = immigration, E = emigration, f = fed, s = starved, y = yes, n = no, 1 = 1%/day, 10 = 10%/day. All data shown are the average of 50 runs. Means-only runs were started with enough food for the 15 nudibranchs for 1 day, normal-distribution runs with enough for seven nudibranchs for 1 day. All  $t_d$  values are significant ( $P < 0.0001$ ).

Exp.	S		I		E		Means-only case				Normal-distribution case			
	f	s	f	s	f	s	$t_{N=0}$	$N_{max}$	$N_{end}$	$t_d$	$t_{N=0}$	$N_{max}$	$N_{end}$	$t_d$
$S_0I_0E_0$	n	n	n	n	n	n	49.2 (0.4)	4643.2 (55.1)		24.4 (0.3)	51.1 (1.6)	1410.4 (637.0)	0.5 (0.5)	45.9 (0.8)
$S_cI_0E_0$	y	y	n	n	n	n		4616.1 (60.1)	34.0 (0.0)			928.8 (77.9)	44.0 (0.6)	
$S_cI_0E_s$	y	y	n	n	n	10		3221.2 (42.4)	14.9 (0.2)			473.3 (116.0)	20.5 (0.4)	
$S_fI_0E_s$	y	n	n	n	n	10	48.4 (0.2)	3240.0 (35.0)		24.9 (0.1)	42.9 (1.2)	299.5 (79.4)		30.7 (0.6)
$S_cI_cE_c$	y	y	y	y	1	1		881.5 (8.8)	735.3 (7.4)			550.0 (9.1)	439.9 (10.0)	
$S_cI_cE_c$	y	y	y	n	1	10		228.6 (7.3)	14.8 (0.1)			104.2 (4.6)	21.2 (0.5)	
$S_fI_cE_c$	y	n	y	n	1	10	27.0 (0.1)	241.1 (7.7)		24.1 (0.1)	35.2 (0.4)	116.2 (6.1)		32.7 (0.4)

successional stage species (Standing, 1976; Harris et al., 1985). Predation on grazers within early colonists could lead to persistence of early colonists to inhibit succession or at least alter the successional sequence to other species (Standing, 1976).

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